On the Irritability of the Fronds of Asplenium bulbiferum, *with Special Reference to Graviperception.*

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[Plate 3.]

1. *Introduction.*

Our knowledge of the phenomena of irritability in vascular plants is largely confined to Angiosperms. Very little work seems to have been done on Pteridophytes; and from his few observations on fern fronds, Darwin [(1), p. 509] even doubted if they possessed any power of response to gravity.

In a preliminary account (4) of the distribution of the statolith apparatus in plants, I mentioned that it was present in young fern fronds, and I have since found that this was partially known to Dehnecke (3). He referred to fern fronds as possessing non-assimilating chlorophyll grains resting on their physically lower cell walls; but he did not connect these grains with the perception of gravity, nor, so far as I am aware, have they ever been photographed or indeed noticed since.

An investigation, therefore, of the physiology and cytology of young fern fronds seemed advisable, in order to ascertain if, and how far, any connection could be traced between them. The common plant *Asplenium bulbiferum* proved a very suitable object for detailed study, though many of the observations described have been confirmed by work on other genera.

2. *The Growth and Movements of the Fronds.*

The plants used were grown in pots, generally under bell jars, in rooms each of which had only one window; thus subjecting them to one-sided illumination the direction of which was known. A few control observations were made on plants exposed to all-round illumination, and on others grown in the dark. The latter were very little used, because it was desired to study the behaviour of plants as far as possible under natural conditions. Many series of observations extended over weeks or even months, where prolonged darkness would have proved very deleterious, if not fatal.

The position of a frond under observation was determined by measuring as nearly as possible the angle made by the midrib with the horizontal. This was done by a very simple, but effective instrument consisting of a transparent protractor (A, fig. 1) mounted between two strips of glass (B) fitted upright into a slot in a wooden block (C). The two pieces of glass are held together, and keep the protractor in place, by an ordinary letter-clip (D) at the top. In order to bring the protractor on a level with the frond, it can be lowered by simply pressing it down from above, or raised by pushing it up from below, at the same time opening and holding down the clip to keep the supports in place. The latter are made of glass, so that the whole frond should be visible, and also to secure the easy adjustment of the 90° line of the protractor against the frame of the window—usually quicker than using a plumb line.

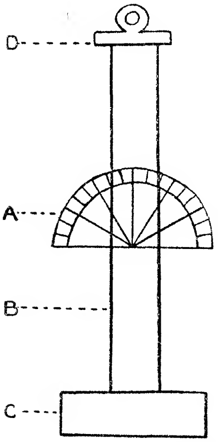

Fig. 1.—Instrument for measuring the angular height of a fern frond.

Three phases may conveniently be distinguished in the life-history of a fern frond; the first or infant phase when the apex of the frond is curled, the second or adolescent phase, from the time when the first leaflets appear beneath the apical coil, till the frond is quite uncurled, when the third or mature phase is reached. Growth cannot be measured as precisely in ferns as in angiospermic stems and roots, owing to the circinate vernation and the considerable individual variation in the process of uncurling. It frequently happens in the middle of the second phase, that the apex is raised very quickly (*i.e.*, in about 24 hours), so that the recorded height shows a greater increment than that due to growth in length. A fern frond, like the organs of angiosperms, shows a grand period of growth. When it first appears above the soil it grows slowly—0·5–1 mm. or so a day. This increases till a young frond 3–10 cm. in height, *i.e.*, in the second phase, may show a daily increment of 4–5 mm. In the third phase, growth slackens, and very gradually ceases altogether.

At least six types of movement are shown by fern fronds:—

(1) *Nutation.*—This is exhibited most strikingly in the second phase of growth, and the results I obtained for Asplenium are very similar to those recorded for *Nephrodium molle* by Darwin [(1), p. 257].

(2) *Rectipetality*, by which I mean the tendency in growth for the different parts of the mid-rib to be in the same straight line. This is sometimes apparently secured in the adolescent stage by an autotropic movement of part of the frond.

(3) *Sagging*, due to the weight of the developing pinnæ, is characteristic of the end of the adolescent and beginning of the mature stage, and gives the frond its final graceful form.

All these movements are slight; the first almost imperceptible to the unaided eye, the second merely occasional, and the third only occurs when growth is nearly over. They will, therefore, not concern us further, and we are left with the three most important movements, due to the following causes:—

(4) *Epinasty*, present throughout the first two periods, causes more or less striking curvatures towards the end of the adolescent phase. The tip of the frond, which may or may not be entirely uncurled, approaches the ab-axial side so that the upper part forms a loop, sometimes almost a complete circle, a position from which it eventually recovers by slight hyponasty.

(5) *Light* has a directive effect upon the frond which varies with the position of the latter, and does not seem to come into play till it is several centimetres in height, *i.e.*, in the middle of the first phase. Curvature is shown most strongly if the frond is placed abaxially to the light, when the apical part generally moves through 90° in the direction of the incident rays (see fig. 2, A).

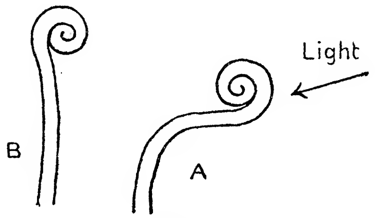

Fig. 2.

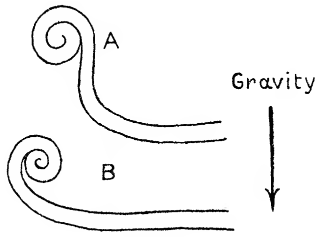

Fig. 3.

Fig. 2.—Explanation in text. (Imagine plane of paper vertical.)

Fig. 3.—Explanation in text. (Direction of light through plane of paper, which is imagined vertical.)

The effect is much less pronounced, and seems to come into play later, if the frond is placed so that the light strikes it laterally (*i.e.*, at right angles to the plane of the paper, fig. 2), when a slight positive movement takes place in the first period, and diaheliotropism, caused by a torsion of the rachis, is shown by the leaflets in the second. If, however, the frond is placed so that the incident rays strike the adaxial surface (fig. 2, B) little or no curvature takes place, but the frond grows approximately vertically well into the adolescent stage, since the effects of light and epinasty balance one another. The backward curve produced by the latter in the second period is considerably lessened.

(6) *Geotropism.*—Irritability to gravity exists from the inception of the frond till near the end of the second phase. It is best studied in fronds placed horizontally and adaxially to the incident light, when the organ will

curve through 90° to bring itself into the vertical. Placed horizontally but abaxially to the light, the frond will move into a vertical plane, at the same time curving towards the incident light. If fronds are placed horizontally, with their ab- or adaxial surfaces uppermost, the subsequent positions assumed are shown in fig. 3. In the former case (A) gravity and epinasty act together; in the latter (B) they are balanced against each other, though gravity seems to have the greater effect of the two, at least in the first phase, since an upward curvature is often produced, though never approaching 90°.

Although very little exact work has as yet been attempted, it is interesting to note that both the latent* and reaction† periods for gravity are probably considerably longer for ferns in general than angiosperms. In one experiment *Asplenium bulbiferum* was compared with Sidalsia sp. The frond of the one and the inflorescence axis of the other, neither unsevered from the parent plant, were placed horizontally in the open at about 27° C. In 4 hours a distinct geotropic curvature was visible in Sidalsia, and 1½ hours more proved sufficient to bring the axis back to the vertical, while no trace of curvature was to be seen in Asplenium. And while I have made few exact measurements‡ of the reaction time for ferns, it has never been as low as 5½ hours, except in Marsilia sp. at 18° C. The latent and reaction periods vary greatly with temperature and perhaps with the season of the year.

An attempt to express the relative effect of the last three factors and their magnitude in the different phases of the life-history of the fern frond is made in fig. 4, though the curves, with the exception of that of growth, are only approximate. In the former case, the ordinates are proportional to heights reached by the fronds on days represented by the abscissæ. The gravity curve rises with the growth of the frond, reaches a maximum in the adolescent stage, and ceases probably before the frond is entirely uncurled. It must, however, be understood that this, like other curves, attempts to express the average of many observations, and does not necessarily hold good exactly for any particular frond. The effect of light is represented by a curve which begins after that of gravity, rises in the second phase to the same height, and ceases probably soon after the beginning of the third phase, and therefore after that of gravity. Finally, epinasty§ starts with the inception of the frond, and is represented towards the end of the second phase higher than gravity or light, since its effect at this time is more pronounced than either, and seems to dominate the situation. It ceases at a period somewhere near the complete uncurling of the frond, but which varies greatly with the individual. Indeed, the last curve must be taken as even more approximate than either of the others, since epinasty is very variable, both in amplitude and the time of appearance and disappearance of its remarkable expression towards the end of the second phase.

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* The time elapsing between the first presentation of the stimulus and the beginning of the response.

† The time elapsing between the first presentation of the stimulus and the end of the reaction.

‡ The duration of these periods is now under investigation by my student, Miss F. M. O. Waight.

§ The subsequent relatively slight hyponasty is included here for convenience under the term epinasty.

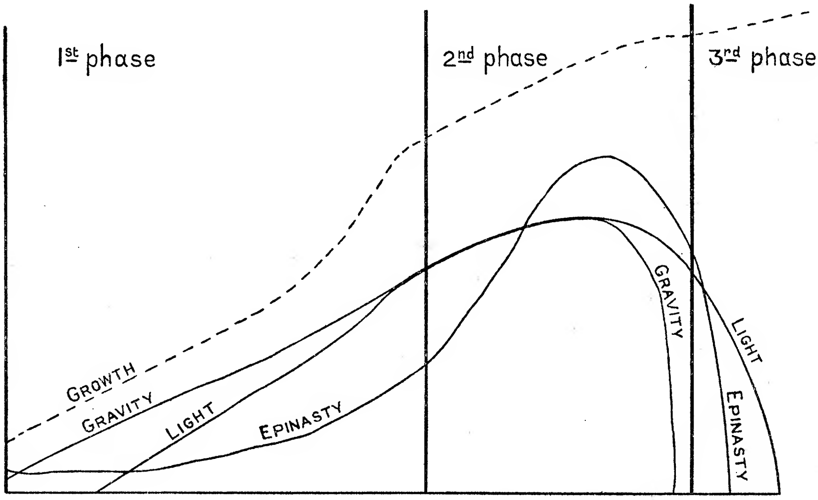

FIG. 4.—For explanation see text.

It is important for our purpose that the time at which geotropic irritability ceases should be ascertained as nearly as possible, but in actual practice this is very difficult, as the hyponastic curve is apt to simulate that due to geotropism, and the matter is complicated by the individual variability of the frond, which is most apparent in the very unstable adolescent stage. It seems at least certain that growth continues after the cessation of geotropic irritability, the frond being at this time only 70–80 per cent. of the length finally attained.

The fern frond is in many ways the biological equivalent of the angiospermic shoot, and, like it, will bring itself back into the vertical should it be displaced from this position. It accomplishes this by passing the vertical and swinging like a pendulum backwards and forwards till it remains upright in a manner similar to that well known for flowering plants, and originally, I believe, described by Darwin [(2), p. 508]. This takes place if the position of a frond is altered in the first, or in the earlier part of the second phase. Should, however, a frond be placed horizontally towards the end of this period, especially if the conditions are such that the reaction period is long, it will probably never reach the vertical, but remain at some angle, continuing its growth in the same straight line. In most cases when this occurs, there is a certain amount of oscillation before the frond becomes fixed in the oblique position.

Fig. 5 illustrates the life-history of an actual fern-frond moving under gravitational stimulus. The dotted line of growth is plotted as before, the other curve showing the rise of the frond, where the ordinates represent degrees. When the frond was only a centimetre or so in height, the pot was placed horizontally, and the frond slowly rose till it was at an angle of 60° with the horizontal. Like most fronds under these conditions, it never reached the vertical, probably in order to avoid the darkness due to the proximity of the soil. When the pot was placed upright, the frond attained the vertical position. Again placed horizontally, the frond rose to an angular height of 70° and then dropped. This was not due to the cause just explained, since the same thing has occurred in experiments when the pot was upright (see below). The frond is seen to oscillate for some time, and finally to take up a position at an angle of 45°, the recorded deviations from this being well within the limits of experimental error.

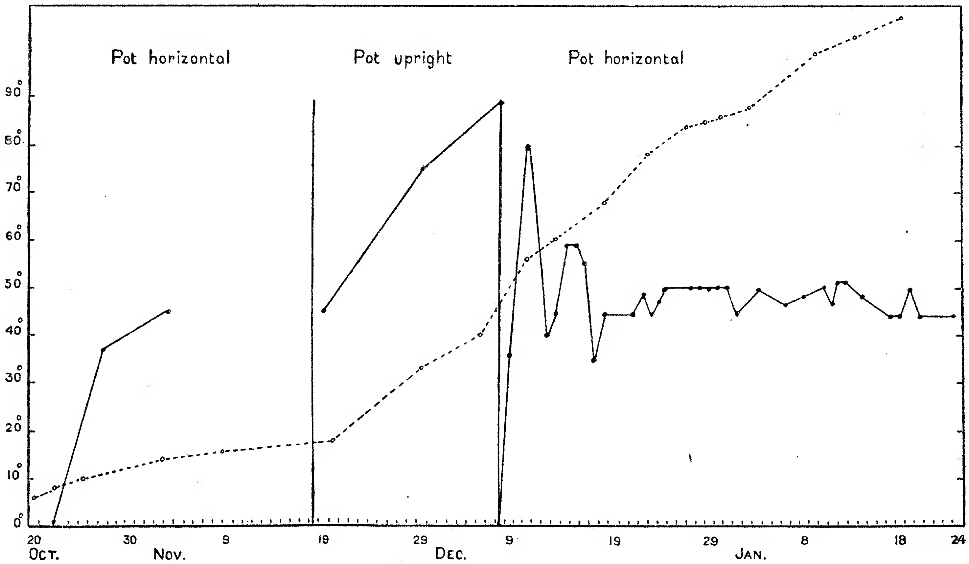

Fig. 5.

Text-fig. 6 is from a tracing made on glass of the actual position occupied by a fern frond on the recorded dates. A complete movement through 90° having been obtained by previously placing the pot horizontally, it was on

February 12 replaced in the upright position, making the frond therefore horizontal. It was slowly rising, till on the 18th it had reached an angular height of 45°. Round that position it oscillated, gradually uncurling, till this was complete on March 2. Soon after, the sagging effect due to the weight of the developing leaflets becomes apparent in the upper part of the frond. It will be seen that epinasty is not well marked in this particular case. As I read it, this record illustrates most of the movements described above, except that due to light, which was shown in the diaheliotropism of the leaflets not represented.

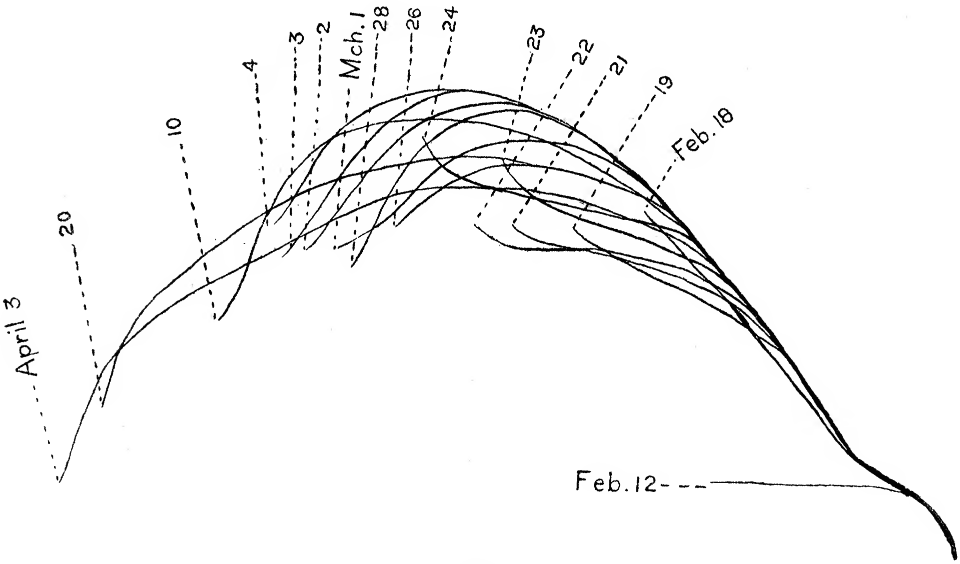

Fig. 6.

3. *The Statolith Apparatus of* Asplenium bulbiferum.

Most attention has been paid to the frond, though some stems have been examined. Starch does not seem to be very abundant in the rhizome of this plant, but was always found at the apex. In one case, in a stem which seemed dormant, very little was present, and it was quite unoriented. Statoliths are, however, always present beneath the rudiments of a developing frond, though some diversity is shown in the cytology of the statocyte. In one case the ground tissue was composed of cells with obvious statoliths, but possessing in addition starch grains round the nucleus, which latter was situated in the middle of the partial statocyte. In another case the nuclei were seen among the statoliths, though probably only loosely attached to them, if at all. This, however, was the only case in which any orientation of the nuclei in *A. bulbiferum* was ever observed.

The very youngest tissue—an actual meristem—never contains statoliths, which is scarcely possible, since little or no sap cavity is as yet developed in which they can lie loose; but, as the young frond develops, the chloroplasts about the bundle at the base become free, and this gradually extends outwards, till practically the whole green part of the ground tissue is composed of chloro-statenchyma (photo. 3). This well-characterised tissue (4) follows, so to speak, the growth of the petiole upwards, by being freshly formed as development proceeds to within a centimetre or so of the apex, and dying away behind as the xylem becomes lignified, and, later still, sclerenchyma is developed. Since more statenchyma is formed apically than dies away towards the base of the petiole, the amount gradually increases, till it probably reaches a maximum as the lower pairs of leaflets develop. It never seems to be found higher than the third or fourth pair, and dies away altogether before the end of the adolescent phase (fig. 7).

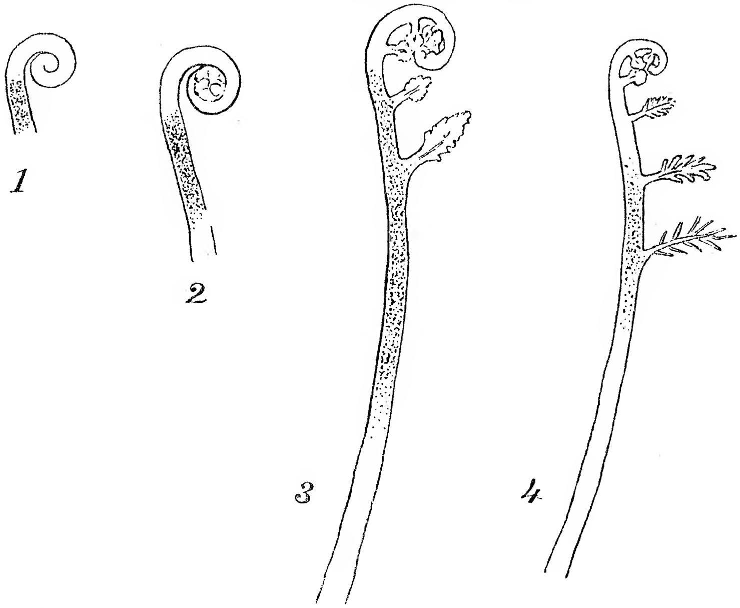

Fig. 7.—Fronds of *Asplenium bulbiferum* increasing in age from (1)–(4). Note that (4) is older morphologically than (3) though smaller. Dotted area indicates amount of statenchyma.

The statolith apparatus is very beautifully shown in the fronds of *Asplenium bulbiferum*. The statoliths are large, bright green bodies full of starch, and apparently indistinguishable from chloroplasts, except that they are completely free from the protoplasm and nucleus. Nearly every cell of the inner ground tissue (at the right time and place, see above) is a statocyte, and practically every chloroplast a statolith, so that we have a very complete, if not the highest, type of apparatus. In good transverse sections cut from fronds laid horizontally for an hour or two, the little heaps of chloro-statoliths may easily be seen with a simple lens lying on the walls which have been lowest. The statocytes are relatively large in cross-section, though shorter than usual in length, being only about twice as long as they are broad.

4. *Summary and Conclusion.*

From the foregoing facts, it will therefore be seen that the life-history of a fern frond of *Asplenium bulbiferum* falls naturally into three periods, characterised not only by external morphology, but by physiological response and cytological differentiation. This may be expressed in tabular form, thus:—

Stage.	Infant.	Adolescent.	Mature.
Frond	Curled	Uncurling	Uncurled.
Heliotropic irritability	Beginning	At a maximum	Ceasing early.
Geotropic irritability........................	Increasing	,, ,,	Absent.
Statocyte tissue	,,	,, ,,	,,

Darwin's failure to recognise apogeotropism for ferns is accounted for by the discovery of (1) the much greater reaction time; and (2) the comparatively early disappearance of geotropic irritability in these plants. In his experiment [(1), p. 509],* the older frond was probably losing its power of response to gravity, and the period of horizontality (46 hours) would not always be sufficient to induce curvature in the case of a frond " with the tip still inwardly curled." Darwin does not give the exact stage of development of this frond, nor the temperature of the experiment—points both of which have been shown greatly to influence the time of reaction.

Next in interest to the demonstration of the existence of both gravi-perceptive power and the possession of statoliths by fern fronds, comes their very close association. This has, of course, been noted for angiospermic shoots (2), but in fern fronds it is more striking. In the first place, a considerable part of the growth of the frond takes place after both its statoliths and its irritability to gravity have disappeared, but when it is *still able to respond to light;* and, again, these disappearances are, as far as can be ascertained, synchronous.

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* I demonstrated apogeotropism in the identical species used by Darwin—*Nephrodium molle*—at Kew Gardens in 1916.

Graphically, this is shown in fig. 4, where a curve for the rise and fall of the statolith apparatus would practically correspond with that of response to gravity—certainly more nearly than with any other. The result of this work may therefore be held to support the view that the possession of statoliths is causally connected with graviperception in plants.

All acknowledgements will be made on the completion of my work on the cytology of the statolith apparatus in plants.

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(2) Darwin, C. (1904). "On the Perception of the Force of Gravity in Plants," 'Brit. Ass. Rep.,' Cambridge.

(3) Dehnecke, C. (1880). "Ueb. nichtassimilirende Chlorophyll-Körper," 'Bot. Zeitung.'

(4) Prankerd, T. L. (1915). "Preliminary Observations on the Nature and Distribution of the Statolith Apparatus in Plants," 'Brit. Ass. Rep.,' Manchester.

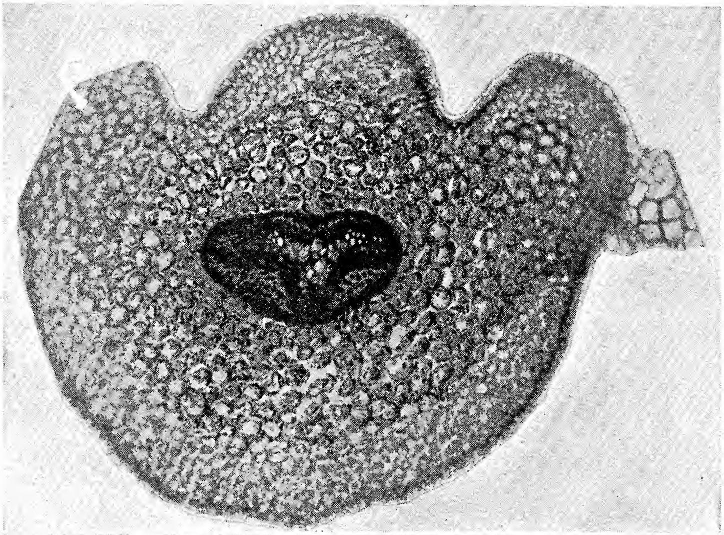
EXPLANATION OF PLATE.

Photomicrographs of transverse sections of a frond of *Asplenium bulbiferum* a little younger than (3) in text-fig. 7.

(1) is taken above the second pair of leaflets, and within the curl. The chloroplasts are scattered in the cells, and there is no trace of statoliths.

(2) cut just above the first pair of leaflets. The ground tissue is transitional between (1) and (3); statoliths are beginning to be formed.

(3) from below the first pair of leaflets—nearly all the cells of the ground tissue are statocytes.



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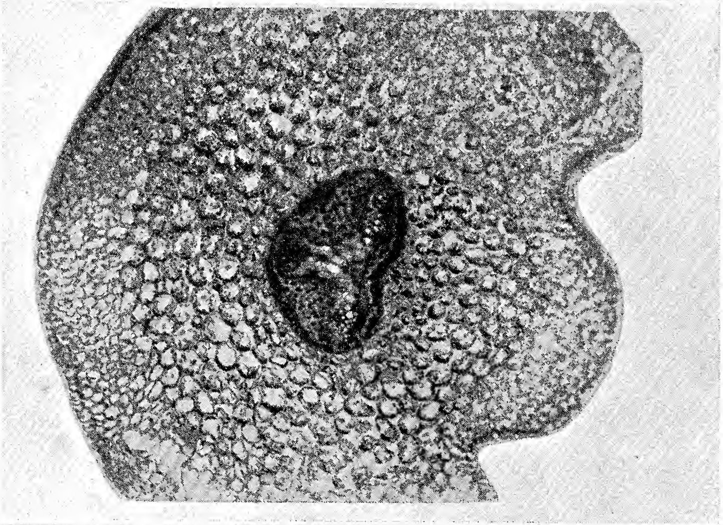

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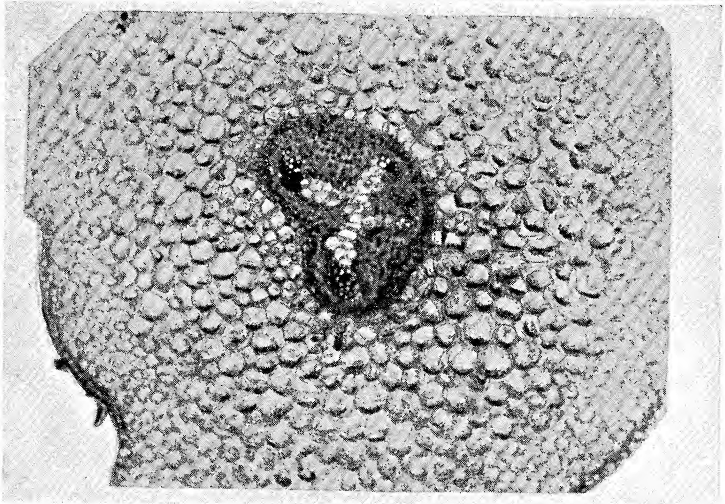

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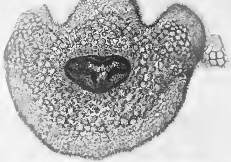

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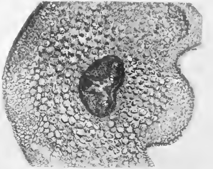

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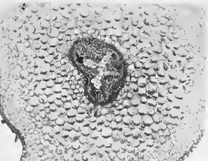

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